

ZOOTAXA ISSN 1175-5334 (online edition)

Article

A second discovery of *Lacertopontonia chadi* Marin, 2011 (Crustacea: Decapoda: Palaemonidae), with remarks on its systematic position

CHARLES H.J.M. FRANSEN¹ & BASTIAN T. REIJNEN²

¹Department of Marine Zoology, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands. E-mail: Charles.Fransen@naturalis.nl

²Department of Marine Zoology, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

E-mail: Bastian.Reijnen@naturalis.nl

Abstract

A second discovery of the cockscomb oyster associated shrimp species *Lacertopontonia chadi* is recorded from Sabah (Malaysia). The material is compared with the type description and paratypic material. The systematic position of the genus is reevaluated on the basis of morphological and molecular data focusing on the genera *Conchodytes* and *Chernocaris*. It is concluded that *Lacertopontonia* and *Chernocaris* fall within the present definition of *Conchodytes* and should be regarded as synonyms of the latter.

Key words: Crustacea, Decapoda, Palaemonidae, Lacertopontonia, Conchodytes, Chernocaris, taxonomy, phylogeny

Introduction

A new genus and species of bivalve associated pontoniine shrimp, *Lacertopontonia chadi* Marin, 2011, were recently described on the basis of three specimens found in association with the cockscomb oyster *Lopha cristagalli* (Linnaeus, 1758) (Bivalvia: Ostreidae) at Lizard Island, Queensland, Australia.

During a survey of pontoniine shrimp diversity in the framework of the Semporna Marine Ecological Expedition (SMEE) (Kassem *et al.* 2012), one male and one ovigerous female were collected from the same host species as the type specimens. When comparing the Semporna specimens with the type description of the species, some morphological discrepancies were noted. These features were checked against the paratype material of *L. chadi* deposited in the collections of Naturalis. Some features were indeed not present or not well developed in the paratypes, others were present though originally not noted or incorrectly described in the type description. As some of these characters were used to define the genus *Lacertopontonia* in relation to closely related genera, its generic status is reevaluated on the basis of both morphological and molecular data.

The current record of the specimens from the Semporna region, Malaysia, considerably extends the known geographical distribution of the species to the North.

The specimens are deposited in Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie (RMNH)) and the Zoological Collection of the Oxford University Museum of Natural History (OUMNH.ZC). Post-orbital carapace length (pocl) is used as the standard measurement of size and indicated in mm.

Materials and methods

Sample collection. Specimens were collected during fieldwork at the Seychelles (1992), Indonesia (2005, 2009), Vanuatu (2006), and Malaysia (2010), representing a subset of species known to live in association with bivalve mollusks and solitary ascidians. The emphasis is laid on species supposed to be closely related to *Lacertopontonia chadi* (see Marin 2011), e.g. *Conchodytes* spp. and *Chernocaris placunae* Johnson, 1967. Specimens were

preserved in 75% ethanol. Representatives of the pontoniine genus *Palaemonella* were selected as outgroup. Data for specimens studied are given in Table I. Tissue samples, derived from eggs or pleopods, were preserved in ethanol before DNA extraction. Voucher specimens are stored in the collection of Naturalis Biodiversity Center.

Molecular analysis. Total genomic DNA was extracted from eggs or pleopods using the DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany). Incubation lasted overnight for approx. 16 hours. The volume in the elution step was decreased to 120 μL to increase the final DNA concentration. For amplifying mitochondrial COI sequences with a polymerase chain reaction (PCR), the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) were used: 5'-GGTCAACAAATCATAAAGATATTGG-3' and 5'-TAAACTTCAGGGTGACCAAAAAAT CA-3'. The PCR conditions were as follows: 1 min. at 95°C for initial denaturing, followed by 39 cycles of 5 sec. at 95°C, 1 min. at 48°C, 1 min. at 72°C with a final extension for 5 min. at 72°C. Each PCR consisted of 2.5 μL CoralLoad PCR buffer (10x; containing 15mM MgCl₂) (QIAGEN), 0.5 μL dNTP's (2.5mM), 1.0 μL of each primer, 0.3 μL Taq DNA polymerase (5 units/μL) (QIAGEN). PCR reactions were performed in volumes of 25 μl. Sequences were generated on an Automatic Sequencer 3730xl at Macrogen, Amsterdam. The obtained sequences were edited in Sequencher (vers. 4.10.1) and aligned with the aid of ClustalW Multiple alignment (vers. 1.4, Thompson *et al.* 1994) incorporated in Bioedit (vers. 5.09, Hall 2001). Of 648 total aligned sites, 269 were variable and 258 were informative for maximum parsimony (MP). Sequences were deposited in GenBank (accession nos. given in Table I).

Data analysis. A minimum evolution (ME) analysis was performed using MEGA 5.05 software (Tamura *et al.* 2011) with 2000 bootstrap reiterations. The best-fitting model for sequence evolution (HKY+I+G) of the COI dataset was determined by jModelTest (vers. 0.1.1., Posada 2008), selected by the AIC (Akaike Information Criterion), and was subsequently applied to the maximum likelihood (ML) analyses with PAUP* (vers. 4.0b10, Swofford 2003) with 2000 bootstrap reiterations. A maximum parsimony (MP) tree was constructed using PAUP* with 2000 bootstrap reiterations of a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping, and 10 randomly added sequence replications. The transition/transversion bias was estimated using the MEGA 5.05 software (Tamura *et al.* 2011). Transversions were weighted 3.14 times compared to transitions to correct for different substitution rates.

Results

Palaemonidae Rafinesque, 1815

Pontoniinae Kingsley, 1879

Lacertopontonia Marin, 2011

Lacertopontonia chadi Marin, 2011 (figs. 1, 2)

Lacertopontonia chadi Marin, 2011: 57-68, figs 1-7.

Material examined. 1 ovigerous female (pocl. 5.1) RMNH.CRUS.D.53857, 1 male (pocl. 3.8) OUMNH.ZC.2012-01-0064; stn SEM.14, Malaysia, Sabah, Ligitan Island, Ligitan 2, 04°09'35.8"N 118°52'22.2"E; 3 Dec. 2010; depth 15 m; inside *Lopha cristagalli* encrusted by a red sponge; collected by Charles H.J.M. Fransen. Paratypes: 1 ovigerous female (pocl. 5.0), 1 male (pocl. 4.0) RMNH.CRUS.D.54783; Australia, Great Barrier Reef, Lizard Island, lagoon, Channel, st. LI10–022, 14°41.435 S 145°27.912 E; 28 Aug. 2010; depth 14–15 m; in wash-out from bivalve *Lopha cristagalli* growing on sea whip; collected by Chad Buxton.

Comparison with type-material. The Sabah material generally corresponds to the type description by Marin (2011). Several dissimilarities were noted in the present material.

The cutting edge of the fixed finger of both major and minor second pereiopods in both the Sabah male and female have the posteriormost tooth shallow and rounded, with many small simple denticles (fig. 1A, B). In the paratype male and female in the RMNH collections this feature is also present although erroneously described and figured by Marin (2011: 67, figs. 5D, E; 6B-F) as: "fixed finger (pollex) with two triangular acute teeth in

proximomedial part". Figure 1C shows the chela of the second pereiopod of the male paratype, originally figured by Marin (2011: fig. 6d).

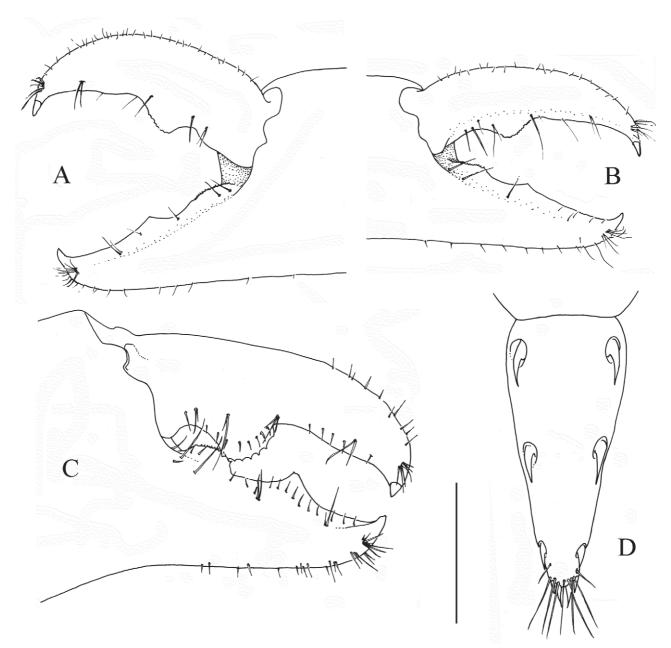


FIGURE 1. *Lacertopontonia chadi* Marin, 2011. A, B, D, male (RMNH.CRUS.D.53857), Semporna; C, male paratype (RMNH.CRUS.D.54783), Lizard Island. A, second pereiopod, left major chela, median view; B, second pereiopod, right minor chela, median view; C, second pereiopod, right major chela, median view; D, telson. Scale bar = 1.0 mm.

The corpus of the dactylus of the third ambulatory pereiopod of the Sabah specimens, as well as the paratypic specimens, have fewer setae than drawn by Marin (2011: fig. 5g). A small, acute, forward directed tooth on a shallow basal protuberance is present on the proximal part of the flexor margin of the corpus of the dactylus (fig. 2A, B). In the paratype material an indistinct tooth on a shallow basal protuberance is visible in the third pereiopod of the ovigerous female, but not illustrated or mentioned in Marin (2011).

In the fifth pereiopod, a rather small shallow angular tooth on a shallow basal protuberance is present on the proximal part of the flexor margin of the corpus of the dactylus (fig. 2C). In the male paratype specimen such a tooth is not present although a shallow basal protuberance can be observed (fig. 2D). The distoventral part of the propodus bears a small articulating spine (fig. 2C). Such a spine has also been observed in the paratype material (fig. 2D), but not illustrated or mentioned in Marin (2011).

Telson with 3 pairs of submarginal dorsal spines and two pairs of distal spines (fig. 1D). The distalmost pair of dorsal spines can also be viewed as a subdistally and submarginally placed lateral pair of spines from the 3 distal pairs of telson spines as described for most Pontoniinae.

The exopod of the uropod is distinctly longer than the endopod. The exopod lacks the distolateral tooth but bears a small mobile distolateral spine. This distolateral mobile spine is present in the paratypes as well (fig. 2E), which contradicts the original description and figure (Marin 2011: 67, fig. 3D, F).

Colouration. As described for type specimens from Lizard Island.

Host. The infestation rate of the shrimp seems low in the Semporna area. After finding the present specimens in *Lopha cristagalli*, about 30 specimens of the host were collected and inspected for the presence of shrimps, without any success.

Systematic position

Morphological data. Marin (2011: 58) states that the present genus can be distinguished from all other pontoniine genera by the following combination of characters: '[1] smooth glabrous body, [2] the absence of antennal and hepatic teeth, [3] broad toothless rostrum turned downward, [4] telson with three pairs of dorsal submarginal spines and two pairs of posterior spines, [5] simple non-spatulate fingers of pereiopod I, [6] short and robust equal pereiopods II with equal fingers, [7] simple dactyli of ambulatory pereiopods, [8] short uropodal exopod (about 1.5 times shorter than uropodal endopod), and [9] the absence of movable spine at the distolateral angle of uropodal exopod.' Two of these features have to be corrected: [7] the dactyli of the ambulatory pereiopods can have a shallow basal protuberance with or without a forward directed tooth, and [9] a small movable spine is present at the distolateral angle of the uropodal exopod.

If we now compare *Lacertopontonia* with other bivalve associated genera and the ascidian associated genus *Odontonia* Fransen, 2002 (see Fransen 2002), as performed by Marin (2011), corrections have to be made with regards to its systematic position in relation to the genera *Conchodytes* and *Chernocaris*.

Characters 1–3, 5, 6, and 8 in *Lacertopontonia* are shared by the genera *Conchodytes* and *Chernocaris*. Of the remaining characters, the presence of [4] a 'telson with three pairs of submarginal dorsal spines and two pairs of posterior spines' is shared with some species in *Conchodytes*, viz. *C. biunguiculatus* (Paul'son, 1875), *C. nipponensis* (De Haan, 1844), *C. philippinensis* Bruce, 1996, as well as the monotypic genus, *Chernocaris* (see Fransen 1994: figs. 3–11; Bruce 1996: fig. 6G, H). A distinct basal protuberance [character 7] with or without a tooth is present in *Chernocaris* and all species of *Conchodytes*, whereas a shallow basal protuberance with or without a tooth is present in *Lacertopontonia*. *Chernocaris* and most species of *Conchodytes* have the dactyli of the ambulatory pereiopods biunguiculate except for *Conchodytes monodactylus* Holthuis, 1852 which has a simple dactylus. The absence of a distolateral tooth and the presence of [9] a small mobile distolateral spine on the uropodal exopod in *Lacertopontonia* are shared by both *Chernocaris* and *Conchodytes*.

The systematic position of *Chernocaris placunae* Johnson, 1964 in relation to *Conchodytes* was described by Johnson (1967) as 'clearly closely related to the genus *Conchodytes*'. Apart from the extreme flattening of the body, two other differences with *Conchodytes* were mentioned: a) the orientation of the chisel edge of the incisor process of the mandible, and b) the spination of the telson. Both these characters, however, do also occur in species of *Conchodytes* such as *C. biunguiculatus*, *C. nipponensis*, and *C. philippinensis*.

Molecular data. The hypothesized phylogeny based on COI (Fig. 3) shows *Lacertopontonia* (and *Chernocaris*) to be nested within a well supported clade with species of *Conchodytes* and clearly separated from other bivalve associated genera and the ascidian associated *Odontonia*. Statistical support for branching within the clade for *Lacertopontonia*, *Chernocaris*, *Conchodytes monodactylus*, and *C. biunguiculatus* is however low.

Within the *Conchodytes*-clade, most species are hosted by members of the bivalve order Pterioida except for *Chernocaris placunae* which is associated with a member of the Pectinioida and *L. chadi* which is associated with a member of the Ostreoida. *Conchodytes tridacnae* Peters, 1952, however, has been recorded from the genus *Tridacna* (order Veneroida) and several species of the Pterioida.

TABLE I. Taxa sampled for molecular analyses with reference to collection registration numbers of voucher specimens, location data, host, and GenBank accession numbers.

				GenBank
Taxon	Voucher spec. reg. nr.	Location	Host class: subclass: order: species	accession #
Lacertopontonia chadi Marin, 2011	RMNH.CRUS.D.53857	Malaysia, Sabah, Semporna area, Ligitan Isl.	Bivalvia: Pteriomorpha: Ostreoida: Lopha cristagalli	JX85697
Conchodytes meleagrinae Peters, 1852	RMNH.CRUS.D.53211	Indonesia, Temate	Bivalvia: Pteriomorpha: Pterioida: Pinctada margaritifera	JX85699
Conchodytes meleagrinae Peters, 1852	RMNH.CRUS.D.53816	Malaysia, Sabah, Semporna area, Ligitan Reef	Bivalvia: Pteriomorpha: Pterioida: Pinctada margaritifera	JX85698
Conchodytes pteriae Fransen, 1994	RMNH.CRUS.D.53846	Malaysia, Sabah, Semporna area, Ligitan Reef	Bivalvia: Pteriomorpha: Pterioida: Pteria spec.	JX85701
Conchodytes pteriae Fransen, 1994	RMNH.CRUS.D.42763	Seychelles, Bird Isl.	Bivalvia: Pteriomorpha: Pterioida: Pteria aegyptiaca	JX85700
Conchodytes biunguiculatus (Paul'son, 1875)	RMNH.CRUS.D.53208	Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands)	Bivalvia: Pteriomorpha: Pterioida: Pinna bicolor	JX85695
Conchodytes biunguiculatus (Paul'son, 1875)	RMNH.CRUS.D.53209	Vanuatu, Santo	Bivalvia: Pteriomorpha: Pterioida: Pinna atropurpurea	JX85696
Conchodytes monodactylus Holthuis, 1952	RMNH.CRUS.D.53212	Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands)	Bivalvia: Pteriomorpha: Pterioida: Pteria ? penguin	JX85694
Chernocaris placunae Johnson, 1967	RMNH.CRUS.D.53216	Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands)	Bivalvia: Pteriomorpha: Pectinoida: Placuna placenta	JX85693
Platypontonia hyotis Hipeau-Jacquotte, 1971	RMNH.CRUS.D.53215	Indonesia, Tidore	Bivalvia: Pteriomorpha: Ostreoida: Hyotissa hyotis	JX85702
Anchiopontonia hurri (Holthuis, 1981)	RMNH.CRUS.D.53832	Malaysia, Sabah, Semporna area, S Kulapuan Isl.	Bivalvia: Pteriomorpha: Pectinoida: Spondylus varius	JX85691
Anchiopontonia hurri (Holthuis, 1981)	RMNH.CRUS.D.53602	Indonesia, Pulau Pulau Gura Ici	Bivalvia: Pteriomorpha: Pectinoida: Spondylus sp.	JX85692
Anchistus miersi (De Man, 1888)	RMNH.CRUS.D.53938	Malaysia, Sabah, Semporna area, Ligitan Isl.	Bivalvia: Heterodonta: Veneroida: Hippopus hippopus	JX85707
Anchistus miersi (De Man, 1888)	RMNH.CRUS.D.53798	Malaysia, Sabah, Semporna area, Ribbon Reef	Bivalvia: Heterodonta: Veneroida: ? Tridacna spec.	JX85704
Anchistus miersi (De Man, 1888)	RMNH.CRUS.D.53806	Malaysia, Sabah, Semporna area, Bumbun Isl.	Bivalvia: Heterodonta: Veneroida: Hippopus hippopus	JX85705
Anchistus miersi (De Man, 1888)	RMNH.CRUS.D.53568	Indonesia, Tidore	Bivalvia: Heterodonta: Veneroida: Tridacna? squamosa	JX85706
Anchistus custoides Bruce, 1977	RMNH.CRUS.D.53795	Malaysia, Sabah, Semporna area, Bumbun Isl.	Bivalvia: Pteriomorpha: Pterioida: Atrina vexillium	JX85710
Anchistus custoides Bruce, 1977	RMNH.CRUS.D.53807	Malaysia, Sabah, Semporna area, Mata Pahi Isl.	Bivalvia: Pteriomorpha: Pterioida: Atrina vexillium	JX85711
Anchistus custoides Bruce, 1977	RMNH.CRUS.D.53810	Malaysia, Sabah, Semporna area, Bumbun Isl.	Bivalvia: Pteriomorpha: Pterioida: Atrina vexillium	JX85712
Anchistus australis Bruce, 1977	RMNH.CRUS.D.53859	Malaysia, Sabah, Semporna area, Ligitan Isl.	Bivalvia: Heterodonta: Veneroida: Tridacna squamosa	JX85708
Anchistus australis Bruce, 1977	RMNH.CRUS.D.53540	Indonesia, Temate, Tanjung Tabam	Bivalvia: Heterodonta: Veneroida: Tridacna squamosa	JX85709
Odontonia sibogae (Bruce, 1972)	RMNH.CRUS.D.53964	Malaysia, Sabah, Semporna area, Horn Reef	Ascidiacea: -: Stolidobranchia: Polycarpa argentata	JX85703
Palaemonella rotumana (Borradaile, 1898)	RMNH.CRUS.D.53973	Malaysia, Sabah, Semporna area, Sipanggau Isl.	Anthozoa: Hexacorallia: Scleractinia: Pectinia paeonia	JX85715
Palaemonella pottsi (Borradaile, 1915)	RMNH.CRUS.D.53928	Malaysia, Sabah, Semporna area, Ligitan Isl.	Crinozoa: Articulata: Comatulida: Comaster spec.	JX85713
Palaemonella pottsi (Borradaile, 1915)	RMNH.CRUS.D.53933	Malaysia, Sabah, Semporna area, Ligitan Isl.	Crinozoa: Articulata: Comatulida: Comaster spec.	JX85714



FIGURE 2. *Lacertopontonia chadi* Marin, 2011, dactylus ambulatory pereiopod. A–C, male (RMNH.CRUS.D.53857), Semporna; D, male paratype (RMNH.CRUS.D.54783), Lizard Island; ovigerous female paratype (RMNH.CRUS.D.54783), Lizard Island. A, third right pereiopod, lateral view; B, same, median view; C, fifth left pereiopod, median view D, fifth right pereiopod, median view; E, right exopod of uropod, distolateral part. Scale bar = 0.5 mm.

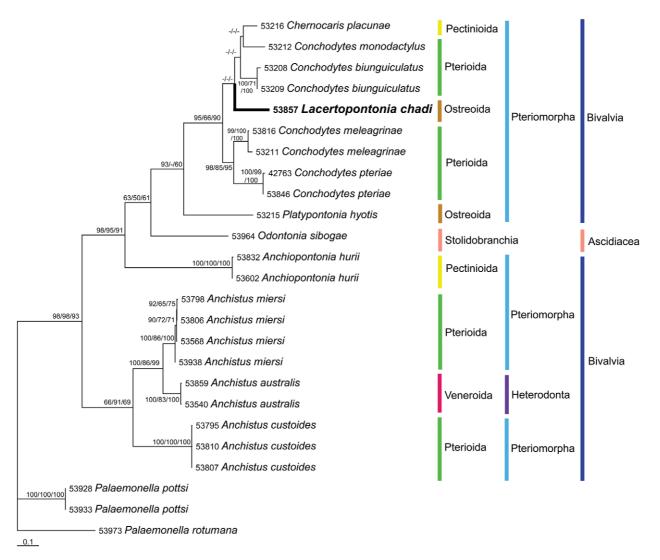


FIGURE 3. Maximum-likelihood tree based on COI sequence data with the GTR+I+G substitution model with host taxa indicated on the right; bootstrap values >50% are shown; bootstrap values are shown in the order ME/ML/MP.

Conclusions

Reevaluation of the morphology of both *Lacertopontonia chadi* based on fresh material as well as the paratypes and *Chernocaris placunae* reveals no distinct, morphological features which would allow both genera to remain valid, separate from *Conchodytes* as presently defined. This position is confirmed by the molecular data. The genera *Lacertopontonia* Marin, 2011 and *Chernocaris* Johnson, 1967 are thus now formally relegated to the synonymy of *Conchodytes* Peters, 1852.

Acknowledgements

Fieldwork for this study was carried out during several expeditions. The R.V. "Tyro" "Oceanic Reefs" Expedition to the Seychelles (1992-1993) was organized by the Nationaal Natuurhistorisch Museum, Leiden (NNM), and the Netherlands Indian Ocean Program. Dr. J. van der Land (NNM) was chief-scientist at these cruises.

The Semporna Marine Ecological Expedition was jointly organized by WWF-Malaysia, Universiti Malaysia Sabah's Borneo Marine Research Institute, Netherlands Centre for Biodiversity Naturalis and Universiti Malaya's Institute of Biological Sciences. Research permission was granted by Economic Planning Unit, Prime Minister's

Department, Economic Planning Unit Sabah, Sabah Parks and Department of Fisheries Sabah. Dr. Bert W. Hoeksema acted as expedition leaders for the biodiversity theme. We are thankful to Sancia van der Meij who helped us in collecting and inspecting host bivalves.

Fieldwork around and in the proximity of Ternate (23 October–18 November, 2009) was undertaken under the umbrella of Expedisi Widya Nusantara (E-Win) of the Indonesian Institute of Sciences (LIPI). Prof. dr. Suharsono, director of the Research Centre for Oceanography (PPO-LIPI), is acknowledged for his support. The research permit was issued by the State Ministry of Research and Technology RISTEK in Jakarta. Dr. Bert W. Hoeksema (Naturalis) and Ir. Yosephine Tuti (PPO-LIPI) acted as expedition leaders. Logistic support was given by Mr. Fasmi Ahmad and his staff of the field research station of LIPI at Ternate, and by Mr. Samar and Mr. Dodi of Universitas Khairun at Ternate.

The 1000 Islands Expedition, September 2005, was organized by the Research Centre for Oceanography, Indonesian Institute of Sciences (PPO-LIPI, Jakarta, Indonesia) and the National Museum of Natural History—Naturalis (Leiden, The Netherlands) (ALW-NWO grant 852.000.50).

The SANTO 2006 Global Biodiversity Survey was initiated by the Muséum national d'Histoire naturelle, Paris (MNHN), Institut de Recherche pour le Développement (IRD) and ProNatura International. Dr. Philippe Bouchet acted as expedition leader for the marine theme (Bouchet *et al.* 2011).

Sammy De Grave is acknowledged for his remarks that greatly improved the manuscript.

Literature cited

- Bouchet, P., Le Guyader, H. & Pascal, O. (eds) (2011) The Natural History of Santo. Patrimoines Naturels, 70, 1-572.
- Bruce, A.J. (1996) Crustacea Decapoda: Palaemonoid shrimps from the Indo-West Pacific region mainly from New Caledonia. *In*: A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM, vol. 15. *Mémoires du Muséum national d'Histoire naturelle*, 168, 197–267.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3(5), 294–299.
- Fransen, C.H.J.M. (1994) Marine palaemonoid shrimps of the Netherlands Seychelles Expedition 1992-1993. *Zoologische Verhandelingen*, 197, 85–152.
- Fransen, C.H.J.M. (2002) Taxonomy, phylogeny, historical biogeography, and historical ecology of the genus *Pontonia* Latreille (Crustacea: Decapoda: Caridea: Palaemonidae). *Zoologische Verhandelingen*, 336, 1–433.
- Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology*, 52, 696–704.
- Hall, T.A. (2001) Bioedit: A User-Friendly Biological Sequence Alignment Editor and Analysis, version 5.09. Department of Microbiology, North Carolina State University, North Carolina.
- Johnson, D.S. (1967) On some commensal decapod crustaceans from Singapore (Palaemonidae and Porcellanidae). *Journal of Zoology, London*, 153, 499–526.
- Kassem, K., Hoeksema, B.W. & Affendi, Y.A. (eds) (2012) Semporna Marine Ecological Expedition. WWF-Malaysia, NCB Naturalis, Universiti Malaysia Sabah, Kota Kinabalu Malaysia, v + 262 pp.
- Marin, I. (2011) *Lacertopontonia chadi* gen. et sp. nov., a new oyster-associated *Pontonia*-like pontoniine shrimp (Crustacea, Decapoda, Palaemonidae) from the Great Barrier Reef of Australia. *Zootaxa*, 2968, 57–68.
- Posada, D. (2008) jModelTest: Phylogenetic Model Averaging. Molecular Biology and Evolution, 25(7), 1253–1256.
- Tamura, K., Peterson D., Peterson N., Stecher G, Nei M. & Kumar S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28, 2731–2739.
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.